

A new genus, *Tuberocandona* gen. nov. (Crustacea, Ostracoda, Candonidae) and past to present ostracod species diversity in Texas (USA)

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Abstract

A new ostracod genus, *Tuberocandona* **gen. nov.**, was collected from Honeycut Hollow Springs, Texas, USA. Morphological comparisons and cladistic analyses showed that the new genus displays several different features (e.g. presence of two tubercles on each of the valves, numbers of A1 segments, shape of A2 claws, shape and presence of two claw-like setae on the clasping organs, absence of d2 and dp setae on T2 and T3, absence of alpha and beta setae on Md, shape of hemipenis) from other genera of the tribe. Including the new species, the number of non-marine ostracods known from inland waters of Texas is now 118 species in 45 genera. With the aim of documenting ostracod biodiversity in Texas (USA) by including fossils, we sought documents published from 1927 to 2022 and were able to list 673 ostracod taxa belonging to 142 genera. Among the fossils, 73 ostracods were the oldest records during the Pennsylvanian period (ca. 310 mya), while there were only 42 taxa reported from the Holocene. The Eocene had the highest number of ostracods (126 taxa). In comparison, the living species had only 18 of 673 taxa that were considered nonmarine forms. There are only six species in common with the fossils and recent records. These results suggest the potential for relatively high ostracod species richness and diversity in Texas. This is indeed strongly supported by the present study and the described new genus and its type species (*Tuberocandona leonidasi* **sp. nov.**).

Keywords

Cladistic analyses, diversity and distribution, Nonmarine Ostracoda, Rheocrene spring

Introduction

Over the last ten years or so, studies on the inland water ostracods of Texas have provided interesting results that highlight unique and high species diversity in the state (Kulköylüoğlu et al. 2021; Kulköylüoğlu and Tuncer 2022). These studies, in total, revealed about 117 ostracod species. Comparing the Texas ostracod list to that of the USA shows Texas contains about 25% to 33% of the USA total (Kulköylüoğlu, pers. obs.). Moreover, this number is also relatively high compared to many other countries in the world such as Turkey (>160 spp.) (Kulköylüoğlu, unpublished data), Italy (156 spp.) (Pieri et al. 2015, 2020), China (154 spp.) (Yu et al. 2009), India (152 spp.) (Karuthapandi et al. 2014), and Germany (126 spp.) (Frenzel and Viehberg 2005). Hence, considering the areas and habitats not sampled and/or not studied yet, the State of Texas will probably contain a much higher species diversity than what we have already discovered. Indeed, contemporary studies in different taxonomic groups (Gibert et al. 1990; Bowles and Arsuffi 1993; Hall et al. 2004; Segers 2008; Hutchins et al. 2020; Gibson et al. 2021) also support this view that the area has high species diversity including epigean, subterranean and groundwater habitats. Studies on the fossil ostracods revealed similar results and even much higher species diversity. These preliminary findings have made us ask how fossil (past) and present (contemporary) non-marine ostracod assemblages and diversity are related. This question is important for at least three reasons: i) aids in understanding the level of correlations between the fossil and live ostracod assemblages, ii) helps to explain how and why replacement of some taxonomic group(s) occurred (if it did) in time, and iii) provides a framework when describing a new species and genus amid other taxa. Inquiring into the literature available, there are no comparative analyses between fossil and current ostracod diversity in Texas. The aims of the present study are 1) to propose a new species and genus *Tuberocandona leonidasi* gen. nov. sp. nov., and 2) to compare and correlate fossil and current numbers of ostracods in the State of Texas (USA).

Methods

Site description

This new species of ostracod was collected from a spring on the privately owned C.L. Browning Ranch in eastern Blanco Co., Texas (Fig. 1). Honeycut Hollow Spring forms the headwaters of Honeycut Creek, which terminates at the Pedernales River during flood events. The flow from this spring returns to the ground around 500 meters downstream (Brune 1981). Abiotic parameters were measured using a Hydrotech compact DS5 with averages calculated for water temperature (22.2 °C), dissolved oxygen (3.1 mg/l), pH (6.6), and electrical conductivity (651 µS/cm) collected during six visits from 13 July to 23 August 2021. The main spring is small, a little over a meter in circumference. This orifice flows out from under what appears to be a bedding plane with maidenhair fern (*Adiantum capillus-veneris* Linnaeus, 1753) along the top edge.

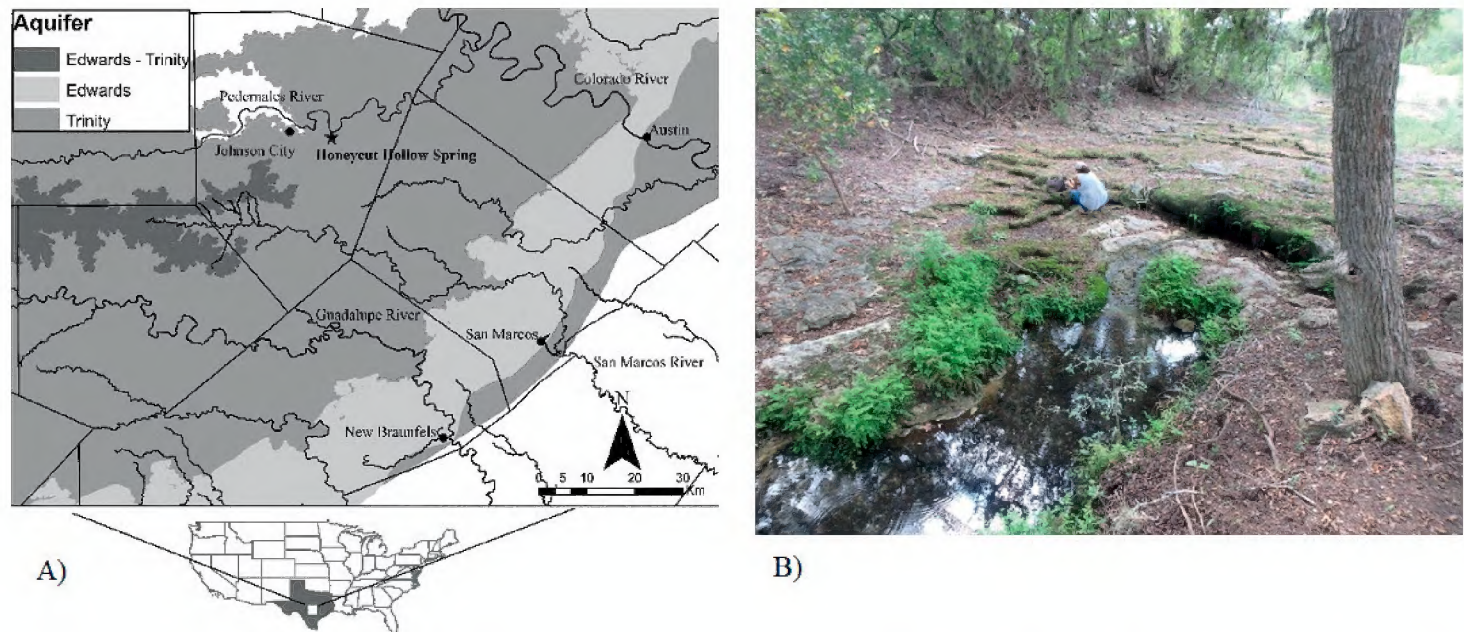


Figure 1. **A** location (*) of sampling site in Texas, USA. **B** detailed photograph of Honeycut Hollow Spring.

Other smaller seeps emerge from along the bottom of this bedding plane. The spring outflow is mainly smooth bedrock; however, gravel substrates are available within the spring opening.

Honeycut Hollow Spring was sampled by placing a 150 μm mesh drift net over the main orifice. The net was lodged into the orifice and surrounded by cobble to maintain the net in place and checked weekly. Samples collected were stored in 95% ethanol and returned to the laboratory where sorting the ostracods from the material was done under magnification removing all aquifer taxa. Sorted samples (e.g. *Stygobromus* sp. (Amphipoda), *Lirceolus* sp. (Isopoda), *Phreatodrobia* cf. *nugax* (Pilsbry and Ferriss 1906) (snail), and harpacticoid copepods)) were also stored in 95% ethanol.

Methodology

Using fine needles, individual species were separated from each other under the SZ-X7 Olympus stereomicroscope. We deposited ostracods in 70% ethanol. Species identification was determined after dissecting adult specimens (i.e., taking the individual specimen to the slide with a glass pipet, measuring the individual, separating soft body parts from the carapace and dissecting the soft parts in lactophenol solution) under a light microscope (Olympus BX-51). Each sample was preserved with a cover slide and labeled with the catalogue number, name, and was stored in the laboratory collection. Line drawings of the soft body parts were made with a camera lucida attached to the light microscope. Scanning Electron Microscope (SEM) was used to take photographs of the carapace and valves at the Department of Geology, Hacettepe University. These samples were kept on the SEM stubs. Although not limited, we generally used common taxonomic keys (e.g. Meisch 2000; Karanovic 2012) for the species identification. During which, the chaetotaxic scheme for the A2 proposed by Martens (1987) and the terminology of the legs were used after Broodbakker and Danielopol (1982) and Meisch (2000). We keep the samples at the Limnology Laboratory of the Biology Department, Bolu Abant İzzet Baysal University, Bolu, Turkey.

Clustering analyses

To determine similarities among the genera of the subfamily Candoninae, we used statistical package program NONA and WinClada, version 1.00.08 (Nixon 2002). During the analyses, including the new genus (*Tuberocandona* gen. nov), a total of 50 genera of the subfamily and two outgroup genera (*Cypria*, *Cyclocypris*) (total 52 genera) were ran to compare 36 morphological characteristics due to their taxonomic importance (Appendix 1) (see Karanovic 2007, 2012; Klkylođlu et al. 2021). After coding the characters in the data matrix, they were weighted for calculating indice values of consistency (Ci) and retention (Ri). Heuristic and Ratchet Island Hopper were used to provide the best fit. This includes 300 replications; 1 best tree to hold, 3 characters to sample, 10 random constraint levels and amb-poly, along with a tree bisection and reconnection method of branching-swapping (Nixon 2002; Karanovic 2007).

Abbreviations: **A1**, first antenna; **A2**, second antenna; **G1–G3** and **GM**, **Gm**, claws on A2; **H**, height; **L**, length; **LV**, left valve; **Md**, mandibula; **Mxl**, maxillula; **RV**, right valve; **T1**, first thoracopod; **T2**, second thoracopod; **T3**, third thoracopod; **UR**, uropod; **W**, width.

Results

Based on the published information (e.g. articles, reports, theses, notes) in Texas, 673 fossil ostracods belonging to 142 genera were reported in the literature between 1927 and 2022 (Table 1). While 655 taxa belong to the marine taxonomic groups, there are 18 ostracod species (Table 2) considered as nonmarine. Six of the 18 non-marine species exist both in fossil and living populations. The oldest 74 fossil ostracod species aged about 310 mya were reported from the Pennsylvanian period (Paleozoic era) while there were about 42 taxa from the Holocene (Table 1). Between them, there were more than 500 taxa distributed among the periods, except Neogene and Triassic (possibly due to lack of data). The highest number of fossil ostracods with 126 taxa were encountered from the Eocene. In contrast to the total of 142 fossil genera, by 2022 only 44 non-marine genera were described from Texas. In addition to these 44 genera, during the present study, we herein propose to recognize an additional genus of non-marine ostracod from Texas, namely (*Tuberocandona* gen. nov.). It is represented by one species (the type species (*Tuberocandona leonidasi* sp. nov.)) (Figs 2–4) with a living population at Honeycut Hollow Spring. The new genus belongs to the tribe Cabralcandonini and portrays clear morphological differences from its other congeners (Fig. 5). Accordingly, this elevates the total number of non-marine ostracods known from Texas to 118 species in 45 genera.

Results indicate that (i) ostracod species diversity is actually and potentially very high in Texas, (ii) most of the fossil taxa belonged to marine ostracods that supports

Table 1. Numbers of fossil taxa reported from 1927 to 2022. Note that the sum of 764 taxa is listed here because several ostracods were reported more than once in different periods or epochs. There are total of 673 single taxa reported once from the state.

Period/epoch	Numbers of occurrence
Holocene Epoch	42
Pleistocene Epoch	6
Early Pleistocene	3
Late Pleistocene	1
Pliocene Epoch	3
Miocene Epoch	8
Oligocene Epoch	4
Eocene Epoch	126
Middle Eocene	70
Paleocene Epoch	15
Cretaceous-Tertiary Period	83
Cretaceous Period	61
Upper Cretaceous	105
Lower Cretaceous	97
Upper Jurassic	15
Middle Permian	51
Pennsylvanian Period	74
Total	764

Table 2. A total of 18 nonmarine fossil ostracods reported from different epochs/periods in Texas. Sources: 1, Swain (1999); 2, Maddocks (1988); 3, Peck (1941); 4, Artusy (1960); 5, Swain (1955); 6, Roth (1933); 7, living forms are known; 8, synonym of *Fabaeformiscandona obtusa* (Bronstein, 1947).

Taxa	Epoch/period	Source
<i>Candona</i> sp.	Early Pleistocene	1
<i>Cyprideis</i> sp.	Early Pleistocene	1
<i>Limnocythere</i> sp.	Early Pleistocene	1
<i>Candona rangliensis</i>	Eocene	1
<i>Cyprideis salebrosa</i> ⁷	Holocene	2
<i>Chlamydotheca llanoensis</i> ⁷	Late Pleistocene	1
<i>Candona</i> sp. indet.	Lower Cretaceous	3
<i>Limnocythere</i> sp.A	Middle Eocene	4
<i>Hemicythere conradi</i>	Miocene	5
<i>Cypricercus?</i> sp.1	Oligocene	1
<i>Darwinula</i> sp.	Oligocene	1
<i>Candona rawsoni</i> ^{7,8}	Pleistocene	1
<i>Cyprideis torosa</i> ⁷	Pleistocene	5
<i>Limnocythere sanctipatricii</i> ⁷	Pleistocene	5
<i>Cypridopsis vidua</i> ⁷	Pleistocene	5
<i>Cyprideis locketti</i>	Pliocene	5
<i>Darwinula aurea</i>	Pliocene	5
<i>Pseudocypridina piedmonti</i>	Upper Jurassic	6

high richness and species diversity, and (iii) the ratio of living/fossil ostracods (118/673) pinpoints the need of specific attention on the living non-marine ostracod fauna. This is an especially important issue for conservation programs future planning.

Taxonomy

Class: Ostracoda Latreille, 1802

Subclass: Podocopa Sars, 1866

Order: Podocopida Sars, 1866

Suborder: Cypridocopina Baird, 1845

Superfamily: Cypridoidea Baird, 1845

Family: Candonidae Kaufmann, 1900

Subfamily: Candoninae Kaufmann, 1900

Tribe: Cabralcandonini Külköylüoğlu et al., 2019

Genus: *Tuberocandona* gen. nov.

<https://zoobank.org/7483A624-5331-41C9-9253-65CEA8E35E5A>

Figs 2–4

Genus diagnosis. Carapace sub-rectangular with two tubercles or nodes on each side (diagnostic character) and surface ornamented with deep hexagonal and pentagonal cells covered with dense spines. Both marginal zones with dense spines. Tubular pore canals with a short sensory seta (diagnostic character), aperture lobate. LV overlaps RV on all sides. Hinge adont. Five adductor muscle scars, one frontal and one mandibular scars visible in about the center of the valves. Inner lamella wide at both ends. LV with an anteroventral node. Selvage absent. A1 6-segmented. Rome and Wouter's organs absent. A2 4-segmented, y1–2 and swimming setae absent. t-setae not transformed in the male. z1-seta absent in males, z2 seta present. Mandibular palp 4-segmented; alpha and beta setae absent (see discussion). Second segment with 4 setae internally, and two setae externally. Third segment with a thin slightly plumose gamma seta. Terminal segment slightly rectangular with one fused claw and one claw-like seta. Maxillula with three endites and two (I–II) segmented palp. Claws on third endite not bristled. Terminal segment of Mxl-palp subsquared. First thoracopod symmetrical in female but transformed into prehensile palps in male. Walking leg (T2) 5-segmented with “d1” seta on basal segment. Cleaning leg (T3) 5-segmented with “d1” seta present. Terminal segment with one long, one medium and one short seta. Uropod well developed with anterior and posterior claws and anterior seta, posterior seta absent. Genital lobe in female rounded without appendages. Zenker organ with 5 whorls. Hemipenis large with outer lobe (lobe a) oval, inner lobe (lobe b) rounded, and large medial lobe (lobe h) subtriangular.

Type species. *Tuberocandona leonidasi* sp. nov. Külköylüoğlu, Ataman, Gibson, Diaz.

Derivation of name. A word with Latin origin “tubero”, meaning “tubercle, lump, node”, is combined with the genus name Candona (gender feminine) due to presence of two tuberculated (noded) alae type of structures on both sides of the carapace.

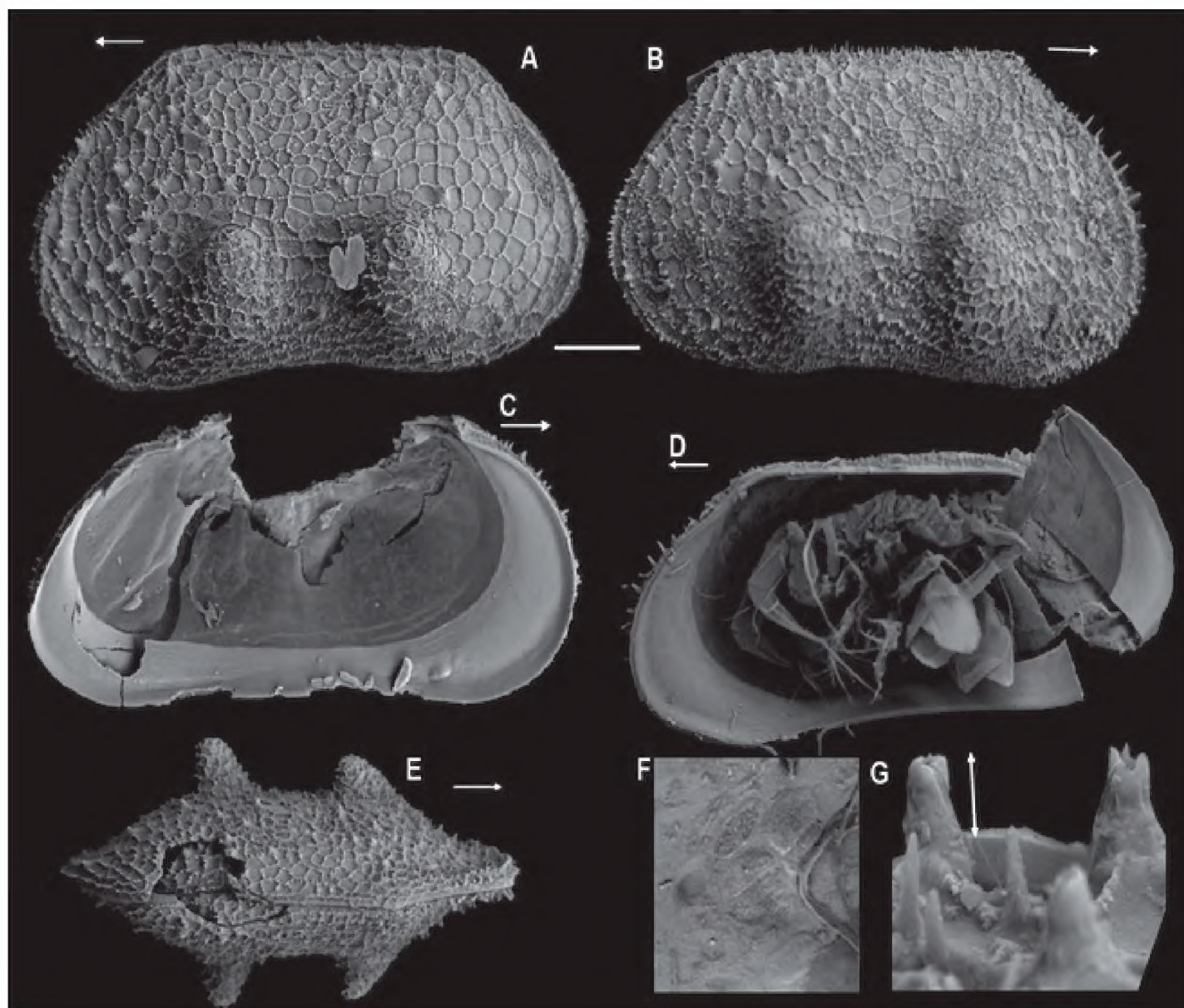


Figure 2. *Tuberocandona leonidasi* sp. nov. **A** LV external view ♂ (Holotype) **B** RV external view of ♀ (Allotype) **C** LV internal view of ♀ (Allotype) (dorsal margin broken) and **D** RV internal view of ♂ with hinge (Paratype) (posteroventral margin broken) **E** dorsal view of ♂ (Paratype) **F** muscle scars of ♂ **G** tubular pore canal of ♂. Scale bars: 70 µm (**A–E**); 10 µm (**F, G**) (two-sided arrow).

***Tuberocandona leonidasi* sp. nov.**

<https://zoobank.org/7A749087-625F-4A7C-95A6-C6490CBDBDD3>

Diagnosis. Holotype. Adult ♂ dissected in lactophenol solution with soft body parts (no: OK-TX-BCo-1) sealed with translucent nail polish; valve kept on a micropaleontological slide (no: OK-TX-BCo-2). Collected from the type locality on 4 and 9 of August 2021 by Peter Diaz.

Allotype. Adult ♀ dissected in lactophenol solution with soft body parts from the type locality (no: OK-TX-BCo-3). Collected by Peter Diaz.

Paratypes. Two ♂ (OK-TX-BCo-4) and two ♀ (OK-TX-BCo-5) mounted and sealed in glass slides, collected from the type locality; total of seven ♀ and four ♂ collected from type locality.

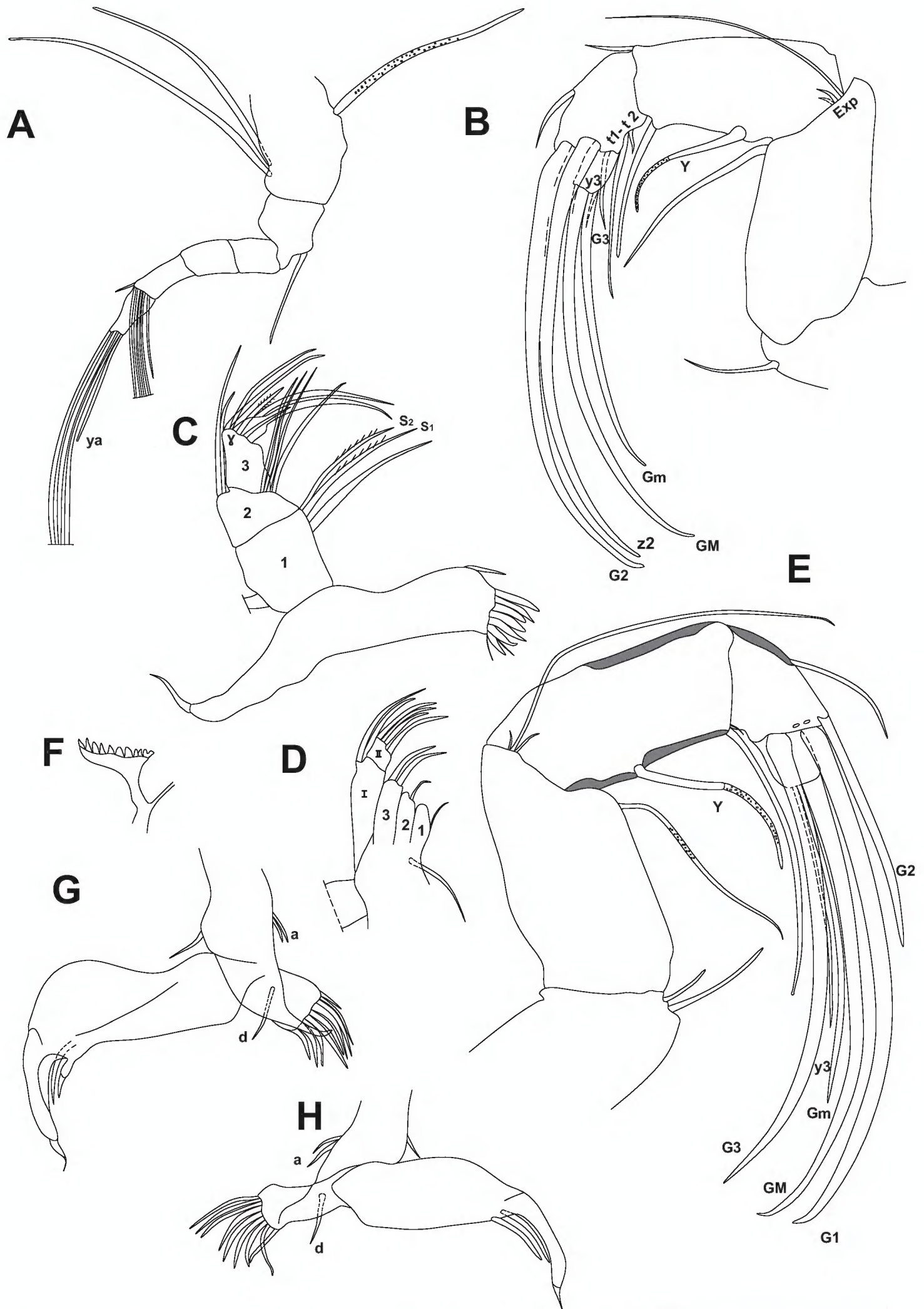


Figure 3. *Tuberocandona leonidasi* sp. nov. **A** A1 **B** A2 **C** Md **D** Mx1 **E** A2 **F** rake-like organ **G** right clasper **H** left clasper. **A–D, F–H** ♂ (Holotype); **E** ♀ (Allotype). Scale bar: 10 µm.

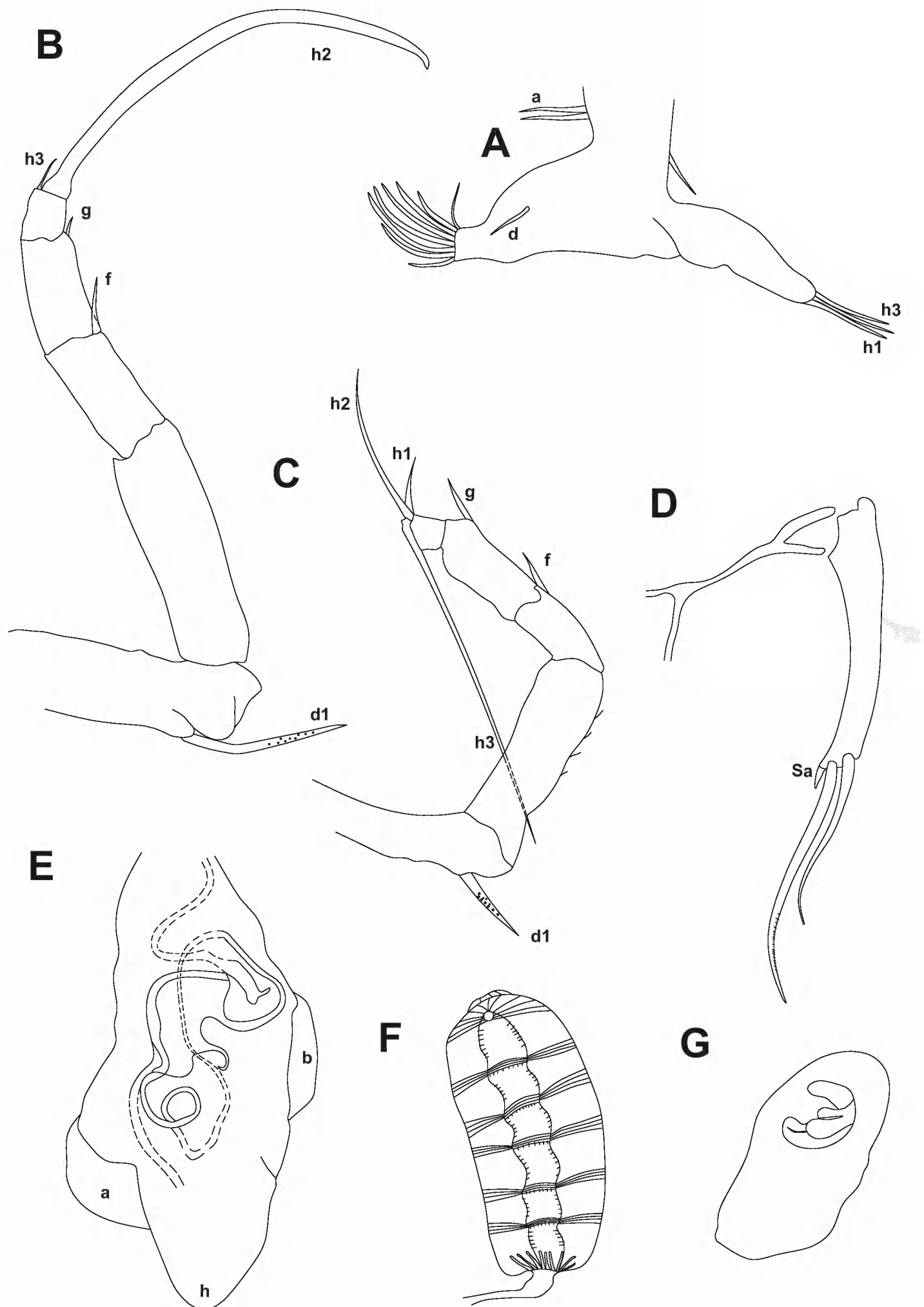


Figure 4. *Tubercocandona leonidasi* sp. nov. **A** T1 **B** T2 **C** T3 **D** uropod and uropodal attachment **E** hemipenis **F** Zenker's Organ **G** genital organ. **A, G** ♀ (Allotype); **B–F** ♂ (Holotype). Scale bar: 10 µm.

Type locality. Perennial headwater of Honeycut Hollow Spring, Blanco County, Texas, USA (30.266319, -98.333497).

Derivation of name. The species is named after the original landowner Caleb Leonidas Browning, Jr as per the current landowner's suggestion.

Description. Male: Measurements (based on midlength). $L=0.51\text{--}0.56$ mm, $H=0.24\text{--}0.27$ mm, $W=0.20\text{--}0.28$ mm ($n=4$). LV overlapping RV anteriorly and posteriorly (Fig. 2A, D–G). Carapace elongate with two well-developed alae type tubercles or nodes on each valve, laterally. In dorsal view (Fig. 2E), both margins pointed. Carapace surface ornamented and covered with spines, especially around each hexagonal cells, pore canals tubular with a thin seta (Fig. 2G). Both margins with stiff spines (Fig. 2D). Dorsal margin almost straight. Calcified inner lamella smooth, without inner list, wide in both margins. LV with internal node anteroventrally, RV smooth. Four large and one small central and two ventral muscle scars located about the center between the tubercles (Fig. 2F). Eyes not visible.

Antennule (A1): Six segmented (Fig. 3A): First segment (base) well-developed with a slightly plumosed long seta on dorsal margin, and two unequally long smooth setae on ventral margin. Second segment with a smooth dorsal-apical seta medium in size. Third and fourth segments without setae. Fifth segment with four long setae and one medium-sized antero-dorsal seta, and one very short ventral-apical seta. Terminal segment with three long and a medium-sized smooth aesthetasc ya (ca. $1/3$ of long setae).

Antenna (A2): Four segmented (Fig. 3B). First segment with a long smooth dorsal-apical seta, reaching halfway of terminal segment. Exopod with one medium-sized and two very small exopodial setae. Second segment without natatory setae. Aesthetasc Y long with two segmented parts extending to end of subterminal segment, proximal part slightly longer than plumosed distal part. Anterior-dorsal seta smooth and long, anterior-dorsal seta very short (ca. $1/4$ of subterminal segment). Penultimate segment with one short seta in dorsal margin, t-1 seta very short, t2 seta long $2\times$ terminal segment all smooth. t3–4 setae absent. Y2-seta not observed. G1 claw absent, G2 claw well developed, G3 claw very short and thin (ca. $2\times$ of terminal segment). Seta z-2 claw-like long reaching tips of G2 claw. Setae z1 and z3–4 not observed (cf. female A2). GM and Gm claws well-developed on terminal segment, Gm claw short about $3/4$ of GM, and y3-seta very short and thin about size of terminal segment. All claws and z1-setae smooth.

Mandible (Md) (Fig. 3C): Coxa with seven robust teeth and thin short setae internally, and dorsal seta short and stout. Palp four segmented; first segment with vibratory plate bearing six plumosed setae, S1 and S2 setae plumosed and unequally long, alpha seta not observed. Second segment with a bunch of four long smooth setae, beta seta not observed. Two (one long and one medium sized) unequally long external setae extending to tips of terminal segment. Penultimate (third) segment with two equally long and smooth external setae, two internal setae unequally long and smooth, gamma seta medium-sized and slightly plumosed. Terminal segment slightly rectangular fused with one claw and one seta-like claw. L:W ratio of terminal segment 1.2.

Maxillula (Mxl) (Fig. 3A): With three small endites and a two-segmented palp, vibratory plate with 12–13 plumosed setae. First, second and third endites with five, five and six setae similar in size (two bristles smooth), respectively. Base of first endite with one long and

slightly plumose seta. First segment of Mx-palp with 2 medial setae. First palp ca. 3× longer than terminal (second) palp. Second segment squarish with 4 claw-like and smooth setae.

Rake-like with 9–10 teeth (Fig. 3F).

First thoracic leg (T1) (Fig. 3G, H): Palps well developed and asymmetrical ending with hooked-like fingers modified into clasping organs. Right palp (Fig. 3G) stronger and robust. Left palp (Fig. 3H) slightly longer than right one. Both fingers ending with a well-developed spine, and two claws. Endite (masticatory process) with 9 to 10 smooth long setae (thicker than usually known). Two unequally long “a” and one “d” seta present, setae “b” and “c” not observed. Vibratory plate with one smooth short seta.

Second thoracic leg (T2) (Fig. 4B): Five segmented with a medium-sized slightly plumose d1 seta on the first segment. Second without seta. Third and fourth segments with unequally long f and g setae, respectively. Terminal segment subrectangular, seta h1 reduced or absent, h2 claw smooth and well-developed, longer than the last three segments. Seta h3 thin.

Third thoracic leg (T3) (Fig. 4C): Five segmented with a well-developed slightly plumose d1, setae d2 and dp absent. Second segment without seta e. Third and fourth segments with smooth “f” and “g” setae, respectively. Terminal segment square three h setae as seen in the Figure.

Uropod (Fig. 4D): Well developed ramus with anterior and posterior claws. Anterior seta short and spine-like, posterior seta absent. Both claws curved and slightly serrated anteriorly. Caudal attachment with one branch.

Hemipenis (Fig. 4E): Large and robust, outer lobe “a” rounded, inner lobe “b” small, medial lobe “h” large and slightly pointing.

Zenker organ (Fig. 4F): With five whorls ending with 15–16 sperm canal.

Color: Translucent to opaque white.

Description of female. Carapace similar in shape of male (Fig. 2B, C). Measurements: L=0.55 mm, H=0.25 mm, W=0.25 mm ($n=2$). G-claws (length ratio $G1 \approx G3 \approx GM > Gm > G2$) ($G2$ ca. 1/3 of $G1$) present on A2 (Fig. 3E). Setae z1–2 thin and very short slightly extending terminal segment, setae z3–4 not observed. Long seta on exopod reaching halfway of subterminal segment (cf. male exopod). Two unequally long and smooth setae present on basal segment (cf. male A2). T1 (Fig. 4A) normally developed, endopod with 2 short (h1, h3) setae, h2 seta not observed. All smooth. Endite with 8–10 apical setae, slightly transformed to claw like. Genital part (Fig. 4G) rounded with a robust genital hook inside. All other parts similar to the males.

Accompanying taxa. *Comalcandona tressleri* Kulköylüoğlu and Gibson, and *Neglecandona* cf. *neglecta* (Sars, 1887).

Discussion

Ostracoda diversity in Texas

Contemporary studies on nonmarine ostracods (Kulköylüoğlu et al. 2011, 2017a, b, c, d, e, 2019, 2021, 2022; Kulköylüoğlu and Gibson 2018; Kulköylüoğlu 2020;

Külköylüoğlu and Tuncer, in press), as well as other taxonomic groups (Reddell and Mitchell 1969; Hall et al. 2004; Segers 2008; Hutchins et al. 2020; Gibson et al. 2021), have clearly shown that the State of Texas contains highly unique species diversity and richness. However, knowledge about fossil fauna is not complete and there are gaps in the evolutionary record that need filling.

During the present study, we compiled all possible fossil ostracod taxa reported from 1927 to April 2022. The 673 fossil ostracod taxa from the Pennsylvanian to the Holocene periods strongly support the view that the area is of high diversity. Among the fossil taxa, there are only 18 ostracods classified as nonmarine (cf. nonmarine ostracod species list of Meisch et al. 2019). Moreover, only six of the 18 (Table 2) still have populations living in aquatic habitats today. Based on earlier studies (Delorme 1991; Forester 1991; Külköylüoğlu 2003), these six species are known to have relatively high ecological tolerances to different environmental variables. All are taxonomically well-known species with records from the Pleistocene to the Holocene (i.e. to the present). The other 12 taxa either do not currently exist or have not been identified at the species level.

During the present study, we found (see Tables 1, 2) that the ratio of the recent taxa in the total numbers of fossils ($18 / 673 = 0.026$) has increased since the last known nonmarine ostracod was reported from Holocene (Maddocks 1988), whereby the current ratio is now ($118 / 673$) increased to 0.175. Such an increase in nonmarine ostracods is apparently related to increasing numbers of studies since the 1930s. However, finding more nonmarine taxa from the Pleistocene to Holocene may also be explained by the fact that most of Texas laid beneath marine waters. Indeed, during most of the late Cretaceous (ca. 140 mya), much of Texas laid beneath marine waters when nonmarine ostracods were not able to establish in the area. Subsequently, nonmarine ostracods appear to have flourished after the intrusion of freshwater habitats (e.g. rivers, springs, underground waters). Finding 122 fossil taxa representing the Eocene Epoch corresponds to this period when freshwater habitats were appearing. According to Salinas et al. (2020) Honeycut Hollow Spring has a relatively stable discharge and long groundwater residence time with a deep flow path. The spring is located on the Cow Creek and Glen Rose limestone formations which is about 115–105 million years old (Young 1974; Barck 1992). The authors stated that water isotope (e.g. deuterium) values were close to constant, indicating that the spring did not respond to precipitation. In other words, the spring has not been affected by environmental changes (e.g. temperature fluctuations) and has been flowing continuously (Salinas et al. 2020). *Tuberocandona leonidasi* gen. nov. sp. nov. appears to be locally adapted to relatively stable aquatic conditions and is possibly endemic to this formation. This is especially important for paleontological studies that aim to explain the past historical environmental conditions. Karanovic (2007, 2012), working on variety of subterranean waters of Australia, postulated that such waters (i.e., springs, underground waters, and/or spring related waters) can carry endemic populations even above the species level. Similar findings are also known for the members of Candoninae reported from South and Central America (Broodbakker 1983), Africa (Martens 1992) and North America (Texas) (Külköylüoğlu et al. 2017a, b, c, d, e).

Taxonomic comments

Cladistic analyses (Fig. 5) illustrated that *Tuberocandona* gen. nov. belongs to the tribe Cabralcandonini but with different features from the other genera of the subfamily Candoninae (Appendix 1). To minimize redundancy, discussion below focuses on those important diagnostic characteristics of the genus and the type species. Therefore, following features are subjected for discussion.

Carapace ornamentation, shape, and pore opening

Presence of two tubercles on each of the valves and spines on the carapace surface along with hexagonal and pentagonal ornamentation are totally unique to the genus. Although it is very common in marine ostracods, several species/genera of the subfamily portray different ornamentations on the carapace; for instance, there are fine longitudinal striations in the *Undulacandona* reported from groundwater located nearby Lake Biwa in Japan (Smith and Kamiya 2015). In addition to the pits, fine reticulations (cf. *Paracandona*) (Karanovic 2012), wrinkle-shaped ornamentations (see *Rugosuscandona*, *Cabralcandona*) (Külköylüoğlu et al. 2017b, 2019), and even bump-shaped ornamentations (see *Ufocandona*) along with variety of microreticulations (Külköylüoğlu et al. 2017e) are known. However, the formation of tubercles with dense spines such as occur in *Tuberocandona* gen. nov. are not known in the subfamily Candoninae where the carapace is mostly described as smooth, pearly lustre, and/or translucent in appearance (Meisch 2000; Karanovic 2004). According to Liebau (1977), macroreticulations may indicate early evolutionary stages of the taxonomic group. During which, macroreticulation can be reduced and the carapace may become smooth. If this is true, with dense spines and ornamentations *Tuberocandona* gen. nov. may represent one of the oldest lineages of the subfamily. Since it is a new description with limited knowledge about the species, generalization may not be possible now.

As stated above, the carapace shape of the new species has interesting outlines and is probably a good proxy for the adaptation to the groundwater environments. It is argued that if a species has rectangular and(or) triangular carapace shape with the posteroventral margin pointed, it most likely lives in relatively stable aquatic habitats where flow rate is low. This is the case for some Candoninae species (Pipík and Bodergat 2005, 2007; Külköylüoğlu et al. 2021). On the other hand, species with subcircular or oval shape are usually encountered in unstable conditions where fluctuations (e.g. flowing rates, evaporation, water movement actions) in the water body may occur. The shape of *Tuberocandona leonidasi* sp. nov. (rectangular shape with wide tubercles) suggests that its habitat (underground water body in the sampling site) has relatively stable conditions.

Pore openings are unique and differ from other congeners of the tribe Cabralcandonini and other members of the subfamily. Numbers of openings seem to be less than many other species. However, its normal pore openings may be longer (range 7–10 μm) than many other species. For example, in *Rugosuscandona scharfi*, height of the canal was between 0.25 and 0.30 μm (Külköylüoğlu et al. 2017b). Also, the

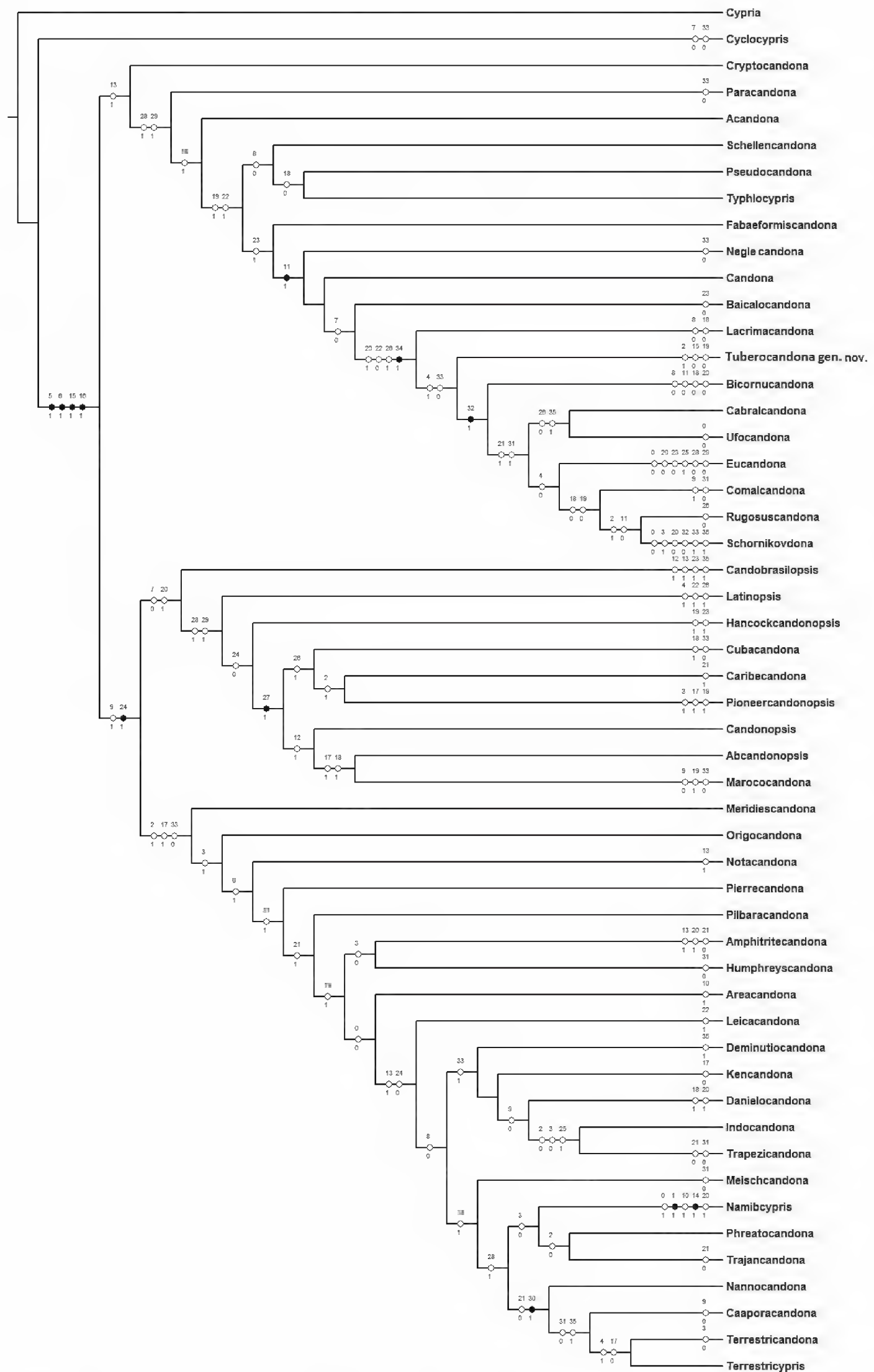


Figure 5. Clustering relationships among the 50 genera of Candoninae (plus two outgroup genera) including the new genus *Tuberocandona* gen. nov. See details in Appendix 1.

aperture of some pores is lobate, which is a character that is not known in any of the Candoninae members. Compared to the diameter of the pore, sensillum is very thin. Among the species of the tribe, *R. scharfi* has similar pore openings but much smaller and more abundant in numbers. Like the new species, *R. scharfi* was reported from groundwaters of the Edwards and Trinity associated aquifers.

Soft body parts and limb chaetotaxy

The new genus along with its type species has different and unique soft body parts and chaetotaxy in the limbs. The tribe Cabralcandonini covers species with five (*Schornikovdona bellensis*) (Külköylüoğlu et al. 2017d) to seven (e.g. *Lacrimacandona wisei*) ((Külköylüoğlu et al. 2017a) segmented A1. Having a 6-segmented A1, the new genus shows similarity to *R. scharfi*. Such reductions in some chaetotaxy of the soft body are known in some other species (Karanovic and Marmonier 2003; Higuti and Martens 2012; Smith and Kamiya 2015; Külköylüoğlu et al. 2017a, b, c, e). Therefore, those characters can illustrate derived character states (Danielopol 1980, 1982).

Sexual dimorphism in the A2 chaetotaxy is common in candonid species (see e.g. Meisch 2000; Karanovic 2007). This is also the case in the new genus (cf. Fig. 3B, E). For this reason, the lengths of the A2 claws are worth more discussion. *Tuberocandona* gen. nov. has long A2 claws which are almost equal or slightly longer than the length of all segments. Similarly, long claws illustrated in some other candonids (e.g. cf. *Ufocandona*) seem to be suitable for subterranean water conditions (Danielopol 1980). The exopodial plate of A2 carries one long and two very short setae both in males and females in the new genus (and species). This is similar in *C. tressleri*.

The t-setae (usually t2 and t3 setae) on A2 of many male candonids (e.g. *Schornikovdona*, *Lacrimacandona*) are transformed into a bristle-type that may be used during sexual courting. However, the t-setae are not transformed into bristles in the new genus like in *Rugosuscandona*, *Ufocandona* and *Comalcandona*. Although it is in a different tribe, similar reductions are also shown in *Indocandona rusti* (Külköylüoğlu et al. 2021), in which t-setae are bristle-type and the exopodial setae includes only two short setae which are barely seen at high magnification. The modifications in A2 mentioned herein may support an adaptive life to benthic subterranean aquatic conditions and/or habitats (e.g. springs) connected to subterranean water sources.

The Md of the new genus has a group of four smooth setae on distal end of segment 3l without alpha and beta setae. Except *Ufocandona*, absence of alpha and beta setae is not known in the tribe; all the species have a gamma seta with variations in length and shape. In the absence of an alpha seta, the new genus resembles *Rugosuscandona* and *Ufocandona*. In contrast, absence of the beta seta is only known in *Lacrimacandona*, *Schornikovdona* and *Ufocandona*. Terminal segment is fused with a thin and long claw in *Tuberocandona* gen. nov. similar to all other five genera discussed in here. Occurrence of a fused terminal claw is also known in members of different genera (e.g. *Phreatocandona*) (Danielopol 1973, 1982). In contrast, the fused terminal claw occurs only in females of *Trajancandona particular* (Karanovic 1999).

Presence of two smooth setae on the third endite of Mxl is also common character among the genera. However, there are sometimes differences between species.

According to the cladistic analyses (Fig. 5), differences in T1 structure were most effective for separating the new genus from others. Besides asymmetry in the male T1, not only the tribe Cabralcandonini but also many (if not all) other candonids appear to have distinguishing dissimilarities on T1. For example, right prehensile palp is very long in *U. hannaleeae*, robust and bumped shape in *S. bellensis*, and almost equal in *R. scharfi*. One of the common characters shared among the species of the tribe is the occurrence of the vibratory plate on T1. Except *R. scharfi*, all species have a single seta. Additionally, *Tuberocandona leonidasi* sp. nov. has two small a-setae when there is one a-seta in *Lacrimacandona* and *Comalcandona* but these setae are absent in *Ufocandona*, *Schornikovdona* and *Rugosuscandona*. Readers are advised to compare occurrence of b, c, and d setae of T1 among the species when differences may not be missed in the hemipenis of the males (Fig. 4E) and Zenker organ (Fig. 4F).

Tuberocandona leonidasi gen. nov. sp. nov. has one d-seta (d1) (e, d2, and dp are absent) on T2 and T3. Appearance of these setae show differences. For example, presence of d1 both in T2 and T3 is common among the species but e-seta of T3, except in *C. tressleri*, seem to be absent in all other species.

The uropod of *Tuberocandona leonidasi* gen. nov. sp. nov. has two well-developed claws and one very short but finger-like anterior seta (Fig. 4D). This structure is different from other species of the tribe. One common character observed in all the genera discussed here, however, is the absence of the posterior seta on the uropod. Thereby, absence of posterior seta is suggested for taxonomic classifications of the genera (and even for the tribe as well).

Conclusion

Based on the detailed morphological and cladistic comparative analyses described above, we conclude that *Tuberocandona* gen. nov. is a new genus of the tribe Cabralcandonini. Also, we report total of 673 ostracod fossil taxa in 142 genera found in Texas. However, we are aware that this number is not definitive and is likely to be increased by future studies. The Pennsylvanian period was the oldest period with 73 ostracod reports. Ostracod diversity (126 taxa) was the highest in the Eocene; however, a sharp decline in the numbers of taxa were seen after this period. It appears that only six species from the fossil record are currently extant. Including the new species described here, the numbers of non-marine living ostracods from the inland waters of Texas increased to 118 in 45 genera. Most of the nonmarine ostracods described from Texas in the last two decades are groundwater species. This trend is continued with the reporting of *Tuberocandona* gen. nov. sp. nov. herein, collected from a spring reliant on subterranean waters. This species description contributed to the ever-growing knowledge of the groundwater diversity of Texas and emphasizes the need for further research and conservation efforts for these often rare and endemic species.

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Cubacandona	0	0	0	0	0	1	1	0	1	?	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Danielocandona	0	0	1	1	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Deminutiocandona	0	0	1	1	0	1	1	1	*	1	0	0	0	1	0	1	1	1	*	1	0	*	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	
Eucandona	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0	1	1	0	1	1	0	0	1	1	0	0	1	0	0	0	1	1	0	1	0	1	0	0
Fabaeformiscandona	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	1	0	0
Kencandona	0	0	1	1	0	1	1	1	0	1	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	
Humphreyscandona	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	*	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Indocandona	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	?	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	
Leicacandona	0	0	1	1	0	1	1	1	1	1	0	0	0	1	0	1	1	1	*	1	0	*	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Marococandona	0	0	*	*	0	1	1	0	1	0	0	0	1	0	0	1	1	1	1	1	1	1	*	0	0	0	0	0	1	1	1	0	0	0	0	0	0	
Meischcandona	0	0	1	1	0	1	1	?	?	1	0	0	0	1	?	?	?	1	1	1	0	1	0	?	?	?	?	?	?	0	0	0	0	0	0	0	0	
Meridiescandona	0	0	1	0	0	1	1	1	*	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Namibcypris	1	1	1	0	0	1	1	?	?	?	1	0	0	1	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	1	1	0	1	0	0	0	0	
Nannocandona	0	0	1	1	0	1	1	?	?	1	0	0	0	1	0	?	?	1	1	1	0	0	0	?	?	?	?	?	1	1	1	1	0	0	0	0	0	
Notacandona	1	0	1	1	0	1	1	1	*	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Origocandona	0	0	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Paracandona	0	0	0	0	0	1	1	?	?	?	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	?	0	0	0	0	
Phreatocandona	0	0	0	0	0	1	1	?	?	0	0	0	0	1	0	?	?	1	1	1	0	1	0	?	?	?	?	?	1	1	0	1	0	0	0	?		
Pierrecandona	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
Pilbaracandona	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	
Pioneercondonopsis	0	0	1	1	0	1	1	0	1	1	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	
Schellencandona	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	
Terrestriacandona	0	0	1	0	1	1	1	?	?	1	0	0	0	1	0	?	?	0	1	1	0	0	0	?	?	?	?	?	1	0	1	0	0	0	0	?		
Terrestriocypris	0	0	1	1	1	1	1	?	?	1	0	0	0	1	0	?	?	0	1	1	0	0	0	?	?	?	?	?	1	0	1	0	0	0	0	1		
Trajancandona	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	
Trapezicandona	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	0	*	0	0	0	0	0	1	0	0	0	0	0	0	0	*	0	0	0	
Typhlocypris	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	*	0	0	
Pseudocandona	0	0	0	0	0	1	1	1	*	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	
Latinopsis	0	0	0	0	1	1	1	0	1	1	?	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	
Rugosuscandona	1	0	1	0	0	1	1	*	*	0	0	0	0	*	0	1	1	0	0	0	1	1	0	1	0	0	0	0	1	1	0	1	1	0	1	0	0	
Ufocandona	0	0	*	*	1	1	1	0	1	0	0	1	0	*	0	1	1	0	1	1	1	1	1	0	1	0	0	0	0	1	1	0	1	1	0	1	1	
Cabralcandona	1	0	0	0	1	1	1	0	1	0	*	1	0	*	0	1	1	0	1	1	1	1	1	0	1	0	0	0	0	1	1	0	1	1	0	1	1	
Lacrimacandona	0	0	0	0	0	1	1	0	0	0	0	1	0	*	0	1	1	0	0	1	1	0	0	1	0	0	1	0	1	1	0	0	0	1	1	0	0	
Schornikovdona	0	0	1	1	0	1	1	1	*	0	0	0	0	*	0	1	1	0	0	0	0	1	0	1	0	0	1	0	1	1	0	1	0	1	1	1	1	
Bicornucandona	1	0	0	0	1	1	1	0	0	0	0	0	0	*	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	1	0	
Comalcandona	1	0	0	0	0	1	1	0	1	1	0	1	*	1	0	1	1	0	0	0	1	1	1	1	0	0	1	0	0	1	1	0	0	1	0	1	0	
Hancockcandonopsis	0	0	0	0	0	1	1	0	1	1	*	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	
Candobrasilopsis	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	1	1	0	0	0	1	0	?	1	1	0	0	?	0	0	0	0	0	0	1	0	1	